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THE FOSSIL GALL RECORD: A BRIEF SUMMARY

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Abstract.—The current status of the fossil gall record is discussed. Significant specimens are highlighted. Despite limitations of the record, available specimens indicate that the gall-forming habit in insects developed to richness in the Tertiary with several relationships stable since the Pliocene (13 mya). Apparent lacunae in the record are discussed.

The history of galls and gall formers has been studied using at least two approaches. The first is to consider the present day distribution of gall-forming insects in light of what is known about land mass distribution and movement. This paleobiogeographic method may provide information needed to reconstruct events without reliance on the admittedly spotty fossil record. For example, the most thorough paleobiogeographic examination of an extant gall-forming taxon suggests a constancy in morphology and habit since the Eocene (50 million years ago) in a species of seed and bract galling cecidomyiid (*Semudobia skuhravae* Roskam) (Roskam, 1979; Gagné, 1984). Once evidence from both biogeography and fossils is brought to bear on the *same* examples, we can expect more complete reconstructions than are presently possible using either tool alone.

As indicated, the second approach to studying gall history is to examine the fossil record. Although several (25 total) accounts of fossil galls have been published, no examination of the assembled record has been made. The purpose of this and another paper (Larew, (a) in press) is to provide a brief summary using paleobotanical evidence of the fossil gall record's status and implications. The fossil record may provide minimum ages of gall-forming associations. Ideally, it may also indicate whether the composition and richness of gall-forming taxa have changed over time.

We are undoubtedly biased in our search for and study of fossil galls. We may for example assume that galls of the past looked like those of today, and pass over or be unable to interpret abnormal structures from plant fossils that were in fact galls. Thus our interpretation of the record may be skewed to infer stability of relationships. There are weaknesses in the fossil gall record itself. For example, almost all known fossil galls are two dimensional impressions in which neither the gall-former nor detailed gall structure is preserved. The identity of the preserved host plant or the age of the specimen may be unclear. Descriptions of the specimens or the specimens themselves are often not of the detail or clarity to distinguish a gall from an artifact of preservation. Lastly there is a scarcity of described specimens.

Despite these limitations fossil galls that have been described provide a skeletal history of gall formation. What follows is a brief review of the highlights of the fossil record. For a more complete description, see Larew ((a), in press).

The oldest known gall was described by Weiss (1904) from tissue sections of *Stigmaria,* which is the root of extinct club moss trees such as *Lepidodendron.* The specimen is from England and is of early Carboniferous age (315 million years ago). Based on the anatomy of root tissue swelling and on the hypertrophied spore-bearing cell in the swelling, Weiss named the gall-former *Urophlyctites stigmariae,* which indicates the similarity in damage seen in the specimen to that caused by the extant chytrid fungus, *Urophlyctis.* Apparently a *Urophlyctis*-like fungus survived the extinction of *Stigmaria/Lepidodendron* and occurs today on the roots of swamp plants and on plants that are periodically flooded such as *Medicago* (Alexopoulos, 1962).

The oldest suspected insect-caused galls are approximately 115 million years old from the upper Cretaceous of Maryland, USA, and were described by Hickey and Doyle (1977) as impressions of leaves of "Sassafras" (there is uncertainty about the host plant's identity although it may be allied with the Platanales). I have found a total of 49 of these galls on leaves collected by Hickey and Doyle. In size, suggested structure and pattern of incidence on the leaves these circular impressions resemble modern day oak leaf spangle galls that are caused by cynipid wasps. The fact that the identity of the fossil host plant is unclear and that oaks are not known from the upper Cretaceous precludes statements about the longevity of this particular relationship. The specimens, however, are significant in their suggestion that structurally sophisticated insect-caused galls were present at a relatively early date.

The most valuable fossil galls are those that were found in the "Miocene (?)" (25 million years ago) lignites of the Duren mines in West Germany (Möhn, 1960). They are noteworthy because larval and pupal cecidomyiids were found in the gall; the larvae lived in, fed on and presumably galled the seeds within the cones of *Sequoia langsdorfii.* Extant *Sequoia* do not host seed-feeding or galling cecidomyiids. The closely related genus *Taxodium* does (Gagné, 1968). Thus the fossil midge species did not survive the reduction in *Sequoia*'s range, but a closely related midge species survives on a related host plant (Gagné, 1968).

The largest collection of fossil galls (Straus, 1977) includes 34 types of leaf gall impressions from the Pliocene (13 million years ago) of West Germany. Included are 2 fungal, 12 eriophyoid, 1 eriosomatid, 1 aphid, 1 adelgid, 6 cecidomyiid, and 3 cynipid galls and 8 of unknown origins. In 13 cases Straus assigns the fossil gall former to extant genera or species. If he is correct in his identifications then it can be concluded that there was a rich and recognizable gall-forming fauna in the Pliocene on several of the plants that are attacked today.

Recently preserved galls, i.e. those preserved in the last 2 million years, include 2 cynipid-caused acorn galls preserved approximately 15,000 years ago in the La Brea tar pits, Los Angeles, California, USA (Larew (a), in press), and are the only known fossil galls of angiosperm seeds. Even more recently preserved were the cynipid-caused oak leaf galls carbonized and thus preserved at Herculaneum, an Italian city destroyed by the eruption of Mount Vesuvius in A.D. 79. Although these last galls are only about 1900 years old, they are nonetheless significant in that they provide the first tangible clues to the importance of galls in early human

Table 1. Geologic time table with the numbers of galls per period or epoch shown, and gall events given in relation to paleobotanical and paleoentomological events.

Period/Epoch	Beginning of Interval (Millions of Years Ago)	Event	Galls	Gall Event
Holocene	0.01		13	All *Quercus*/cynipid
Pleistocene	1.5–2		3	
Pliocene	5–13		28	Many recognizable galls
Miocene	22–23		7	
Oligocene	37–38		6	
Eocene	53–54	Modern angiosperms	4	
Paleocene	65			
Cretaceous	136	First angiosperms	6	First insect gall
Jurassic	195		1	
Triassic	225	Abundant cycads and conifers		
Permian	280			
Carboniferous	345	Abundant insects and coal forest	1	First gall (fungal)
Devonian	395	First insects		
Silurian	435	First land plants		
Ordovician	500			
Cambrian	570			
		Total	69	

culture. Collection data suggest that the galls were being offered for sale in a shop probably as a source of tannins for medicines or dyes, at the time of the eruption (Larew (b), in press).

A summary of major paleobiological events is shown in Table 1. The number of fossil gall specimens in each period or epoch is provided as are comments about particular specimens. In general the record suggests that as early as the late Paleozoic (Carboniferous), cecidogenetic relationships existed that resemble those that occur today. The gall-forming habit in insects, although seen probably as early as the Cretaceous developed to richness in the Tertiary (the Pliocene, especially) when modern day angiosperms became abundant. From the Pliocene, indications are that many relationships have been stable. According to Opler (1973) fossil evidence of lepidopterous leafminers on oaks demonstrate a similar constancy from the middle Miocene.

There are noticeable lacunae in the fossil gall record. For example, there are no known fossil galls from regions other than western Europe and the United States. This deficiency may in part explain why there are no fossil galls that have been ascribed to thrips or scales; galls caused by these insects are most common today in Asia and Australia. Neither are there reports of fossil galls caused by beetles or moths, despite the suggestion that structurally these are some of the simpler and presumably more primitive insect galls today (Mani, 1964). No fossil flowers or stem galls have been described.

Lastly, although the first land plants are known from the Silurian, the first gall (*Urophlyctites*) does not occur until the Carboniferous, approximately 150 million years later. Was there a time lag of many millions of years between the development of a terrestrial flora and the first occurrence of galls? Or is the fossil gall record incomplete? The last seems more likely. Just as curious is the complete lack of gall specimens from aquatic plants *before* the Silurian. Algae, bacteria, fungi, nematodes, rotifers and copepods form galls on marine and fresh water algae today (Mani, 1964). Although insects presumably arose in the Devonian, insect-caused galls are seen for the first time in the Cretaceous, approximately 250 million years later. The intervening years saw the rise and fall of the great coal forests composed of lycopods and horsetails, and an abundance of cycads and gymnosperms, but to our knowledge no insect-caused galls were formed. Thus, the very early history of galls awaits more complete paleobotanical information.

To date and reconstruct evolutionary events is the goal of paleobiologists. The fossil gall record presently indicates a few key events and suggests many more. Our interest in galls and more generally in insect/plant interactions requires that the record be enriched through a broad and thorough search for specimens.

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